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RESEARCH ARTICLE

A social mechanism facilitates ant colony emigrations over different distances

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ABSTRACT

Behavioural responses enable animals to react rapidly to fluctuating environments. In eusocial organisms, such changes are often enacted at the group level, but may be organised in a decentralised fashion by the actions of individuals. However, the contributions of different group members are rarely homogeneous, and there is evidence to suggest that certain 'keystone' individuals are important in shaping collective responses. Accordingly, investigations of the dynamics and structuring of behavioural changes at both the group and individual level are crucial for evaluating the relative influence of different individuals. Here, we examined the composition of tandem running behaviour during colony emigrations in the ant species *Temnothorax albipennis*. Tandem running is modulated in response to emigration distance, with more runs being conducted when a more distant nest site must be reached. We show that certain individuals are highly active in the tandem running process, attempting significantly more work in the task. Contrary to expectations, however, such individuals are in fact no more successful at conducting tandem runs than their less active nest mates. Instead, it seems that when more tandem runs are required, colonies rely on greater recruitment of workers into the process. The implications of our study are that in some cases, even when apparently 'key' individuals exist within a group, their relative contribution to task performance may be far from decisive.

KEY WORDS: Heterogeneity, Collective behaviour, Self-organisation, Sociobiology, *Temnothorax albipennis*

INTRODUCTION

Spanning a broad range of species and genera, behavioural modification constitutes an essential component of the adaptive repertoires of animals. Examples range from simple Pavlovian responses in mammals (Jenkins et al., 1978), to complex, multi-generational cultural changes in human societies (Kirk, 1996; Inglehart, 1997) and inter-species mutualisms in the social insects (Way, 1963). Common to all of these strategies is the advantage of rapid benefits when compared with the more gradual changes elicited by natural selection alone. Considerable effort has been invested into studying behavioural changes at both the group (Barsade, 2002; Langridge et al., 2004) and the individual level (Shettleworth, 2001). However, the interplay between the two, especially in complex networks, is less well understood (Bornstein and Yaniv, 1998; Franklin and Franks, 2012; Anderson and McShea, 2001; Hunt et al., 2016).

Social insects display complex life history characteristics, underpinned by efficient colony organisation, and thus provide excellent models for studying how group-level behavioural changes are structured through the actions of individuals. This is in no small part due to their propensity for self-organisation, whereby complex processes may emerge without the need for centralised control, an ability that many human systems lack (Camazine et al., 2003). Self-organisation can lead to the formation of adaptive but flexible group behaviours, which often confer additional benefits to colony functioning (Goss et al., 1989). Hence, such behaviours are of interest when attempting to elucidate how multi-level behavioural change is structured. Colony relocation represents one process that is regulated at both the group and individual level in social insects, and, indeed, wide variation exists among species in relation to how migration effort is assigned. Examples range from varying distributions of worker effort within colonies, as seen in the ant *Myrmecina nipponica* (Cronin, 2015), to extreme cases where a single individual is key to overall collective organisation, such as in the queenless Ponerine, *Diacamma indicum* (Sumana and Sona, 2013).

In the ant *Temnothorax albipennis*, emigration behaviour is regulated at the group level to best suit environmental conditions, but relies on individual contributions and information sharing (Franks and Richardson, 2006). Colonies of this species reside within rock cavities in a moderately heterogeneous and unstable environment, and, as such, they frequently have to emigrate to potential new nest sites in order to maintain their protection from external threats (Dornhaus et al., 2004). Before an emigration can occur, however, scouting workers must accumulate within a new nest site until a 'quorum threshold' is reached (Pratt, 2004). A key behaviour in this process is tandem running, in which workers lead their nest mates to the location of a potential nest site or food source (Franklin and Franks, 2012). During a tandem run, the leading worker will maintain intermittent tactile contact between its gaster and a follower's antennae, leading the follower to the desired resource via an often-tortuous journey, and thus informing it of the route (Franks and Richardson, 2006). Previous work has shown that colonies of *T. albipennis* increase their rate of tandem running, defined as the total number of tandem runs in relation to colony size, during emigrations where the target nest site is further away (O'Shea-Wheller et al., 2016). This may be explained by the need to reduce emigration time and thus colony exposure during more distant emigrations (Traniello, 1989), and is elicited by a reduction in the rate of nest discovery (Pratt, 2004). Despite being colony-wide phenomena, tandem running responses are necessarily achieved by perception at the individual level, whereby workers determine that a quorum has not yet been met in a new nest site

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(Pratt, 2004). As a consequence, the individual propensity of ants to engage in tandem running is likely to influence the overall structuring of the process, yet the dynamics of this remain unexplored.

Several potential hypotheses may explain how individuals contribute to an increase in tandem running over longer emigration distances. First, workers that would not usually be involved begin to assist in leading or following tandem runs. Second, a 'core' of the same highly active workers simply lead more tandem runs themselves. Third, a combination of the two may occur. The relative likelihood and significance of such options is uncertain, as previous studies have shown complex and differing structures of work distribution within colonies. Many of the studies conducted to date support the concept that *T. albipennis* colonies have some 'specialist' workers in relation to certain task groups (Dornhaus, 2008; Dornhaus et al., 2008). It has been noted that task propensities are positively correlated within groups of related tasks, e.g. 'foraging' and 'emigration'. Moreover, workers highly active in one task group may be less so in others (Pinter-Wollman et al., 2012), suggesting 'situational specialisation'. Nevertheless, some workers may still be persistently active across all task groups (termed 'elites'), though they constitute only a small proportion of individuals (Pinter-Wollman et al., 2012). In addition, the extent of specialisation may vary depending on colony characteristics; for example, it has been shown that during brood carrying, smaller colonies will employ some specialist workers that are more active than others, while in larger colonies, each active individual contributes more evenly to the process (Dornhaus et al., 2008). Consequently, a greater understanding of how increased tandem running and other behavioural changes occur during more distant emigrations should help to shed light upon the underlying processes that govern group and individual behaviour in a decentralised system.

In this study, we examined several key stages in both short and long distance emigrations at the group and individual level, in an effort to determine how behavioural changes were structured across individuals. Chiefly, we wished to determine whether increases in the rate of tandem running were due to key individuals up-regulating their activity, more workers becoming involved, or indeed a mix of these two. We also tested the hypothesis that workers would alter their average tandem running return speed across emigration distances, as faster return rates would allow ants to recruit other colony members to a new nest more rapidly. Additionally, we attempted to determine whether there was a link between initial scouting behaviour and a worker's subsequent propensity to become actively engaged in emigrations.

We addressed these questions by quantifying colony-level changes, including those associated with tandem running, scouting, average return speed and workforce mobilisation. Then, in order to dissect the processes underlying such changes, we measured distributions of individual scouting, tandem running and movement speed, having uniquely marked all workers within each of the 10 experimental colonies. Furthermore, we identified behavioural sub-groups of workers by categorising individuals in relation to their engagement in only one or both emigration distances. We then assessed differences in attempted and successful per capita tandem running workloads between these groups, to quantify their relative importance to the system as a whole.

MATERIALS AND METHODS

Colonies

We collected 10 colonies of *Temnothorax albipennis* (Curtis 1854) from the isle of Portland, Dorset, UK, on 29 September 2015. Colonies contained between 47 and 187 workers, and between 19 and 130 brood items, and each had a single queen. No specific permission was required for collection, with ants being taken from a disturbed quarry area open to the public. Additionally, no collection permit was required, as *T. albipennis* is not a protected species. In order to minimise the impact of colony removal on the local population and ecology, we used an established rota to vary collection location, based on date.

Colonies were migrated into initial laboratory nests and allowed to acclimatise for a period of 7 days after collection. We maintained them in the laboratory under established conditions (Dornhaus et al., 2004; Franks et al., 2003), with all nests being housed in plastic Petri dishes with Fluon-coated sides. Ants were fed weekly with *Drosophila melanogaster*, and allowed to forage for water and honey solution *ad libitum*.

Marking

The 10 colonies were randomly numbered in order to determine a marking sequence. For each colony in turn, we anaesthetised all workers with CO_2 and painted them with a unique permutation of three colours, one on the thorax and two on the gaster (Fig. 1A). A mounted single hair and microscope were used in order to apply the paint with precision. Markings corresponded to an identification key, allowing rapid determination of individual identity, in addition to total colony populations (Table S1). Care was taken to ensure that CO_2 exposure was kept to a minimum, and there was an interval of at least 48 h between marking and experimental trials, as studies have shown that insect behaviour may be affected after anoxia (Poissonnier et al., 2015). Further precautions were taken to ensure that paint did not cover the gaster tips of workers, as this may impair the use of chemical signalling (Stuttard et al., 2016).

Nest design

We utilised two different nest qualities in our experiment: 'poor' and 'excellent'. Colonies were initially housed in poor quality nests, and allowed to emigrate into the excellent nests during trials. Both designs were composed of microscope-slide lids and bases with a cardboard perimeter sandwiched between the two to create an internal cavity. The area of this cavity was constant across the two nest qualities, measuring 65×35 mm. Poor quality nests had 1 mm high walls, a 6 mm wide entrance and a clear cover, while excellent quality nests had 2 mm high walls, a 1 mm wide entrance and a red filter cover. These differences combined to make excellent nests more spacious, more secure, and darker than poor quality nests, and thus far superior in the ants' assessment (Franks et al., 2003).

Emigration trials

All colonies underwent emigration trials under 'move-to-improve' conditions, in which their original nests were left intact, allowing them to emigrate of their own accord to the superior excellent quality nests (Dornhaus et al., 2004), at distances of 100 and 300 mm (Fig. 1B,C). Twenty emigrations were conducted in total, over a period of 35 days, with each colony performing two emigrations in turn. In order to account for the potential experience effects of multiple emigrations (Langridge et al., 2008), using random assignment, five of the colonies underwent the 100 mm trial first, and five the 300 mm trial first.

Prior to the initiation of each trial, we cleaned 1000×1000 mm arenas with 70% ethanol solution, and illuminated them evenly using the laboratory lighting system (4100 lm, colour rendering index: 85%). Colonies housed in their original poor quality nests

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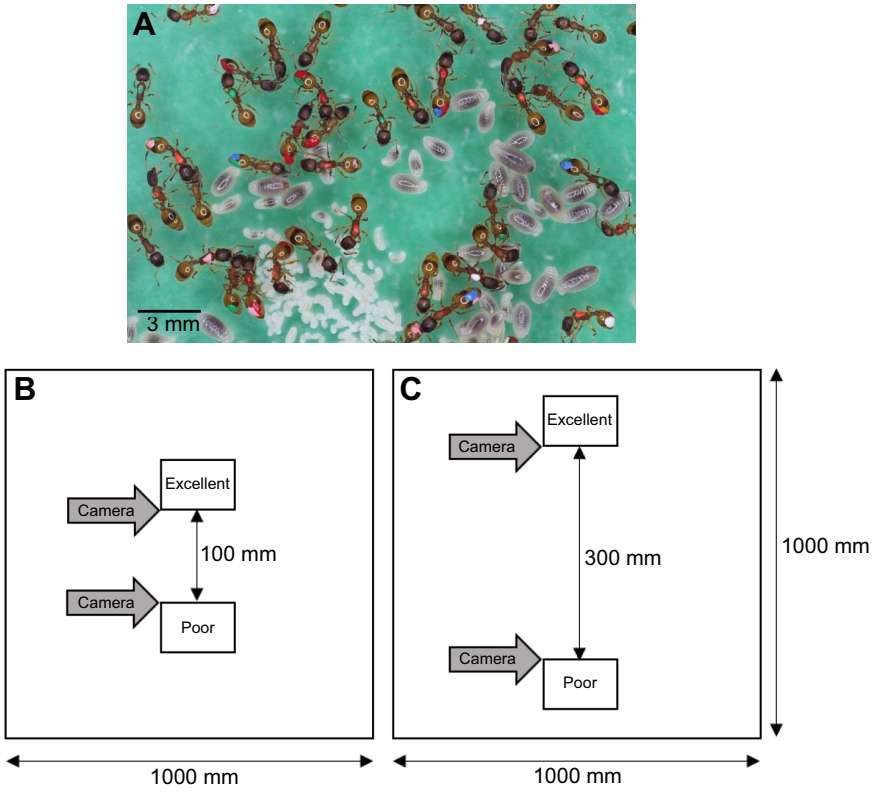

Fig. 1. Experimental setup. (A) Marked *Temnothorax albipennis* workers. Although some are missing paint marks, the numbering system was robust to this. (B,C) Experimental arena setup for the 100 mm trial (B) and 300 mm trial (C). Dimensions indicate actual arena sizes; the figure is for illustrative purposes only and is not to scale.

were then transferred into the arenas and empty excellent quality nests were placed either 100 or 300 mm from them. At the initiation of experiments, the emigration process was observed and we began monitoring scout identities and numbers, tandem leader and follower identities and tandem durations, tandem run success rate at the two different distances, average ant return speed, and the total number of ants in the arena and nests (at 10 min intervals) (raw data are given in Table S2). Additionally, HD video recording equipment (Panasonic HC-X900 series) was set up over both nest sites for the duration of emigrations, in order to facilitate further data analysis (Fig. 1B,C).

Range of assessment factors

Analyses were broadly divided into investigations of the distribution of tandem running among workers, average return speeds, and the effect of scouting propensity on emigration engagement. Within these groups, we examined both colony-level behaviour and that of individual ants (via marking).

To quantify behavioural changes in tandem running distribution, we compared the total number of tandem runs per colony, the percentage colony engagement in tandem leading or following, and the total number of tandem runs per ant. By measuring the total number of tandem runs per individual, we were able to compare the activity of ants that were involved at a single emigration distance with that of ants involved across both emigration distances. This division method was important for testing the hypothesis that the same key individuals would conduct significantly more tandem runs at a longer distance (i.e. those individuals comprising the 'both' group; see below).

To achieve this, workers were divided into two groups; those actively engaged in only one emigration distance (the 'either' group) and those actively engaged in both emigration distances (the 'both' group). Engagement in an emigration was defined as workers conducting scouting, tandem running, or both.

We then compared the attempted and successful per capita tandem running workload of ants using the same division method, in order to account for the different sizes of these groups. Per capita tandem running workload constituted the average amount of tandem running work (leading or following) done by each tandem running worker, as a proportion of the total tandem running work conducted by all workers in a given emigration, and thus was a measure of individual contributions. In concert with the total absolute number of tandem runs conducted by workers, the use of this proportional measure allowed us to determine the relative importance of worker groups in the tandem running process at different distances. Additionally, we tested the effect of the number of attempted tandem runs on an individual's tandem running success.

We quantified average worker return speed across the two emigration distances, pooled by colony. When returning to their old nest, workers take a direct route between sites (Franks and Richardson, 2006), and thus speed was calculated as a function of distance over time. To assess the effect of prior scouting on an individual's propensity to engage in emigrations, we measured scouting effort (defined as the number of ants exploring outside the nest over time) across colonies, and the effect of prior scouting experience (defined as leaving the nest to explore) on a worker's subsequent involvement in tandem running. New nest discovery time, percentage colony involvement in emigrations and quorum attainment time were also analysed.

Statistical analysis

For all colony-level data, we used Shapiro–Wilk tests to check for normality, and hence to inform the application of appropriate statistical tests. Where the data were found to be normally distributed, we conducted either paired or independent *t*-tests. For measures in which the data were not normally distributed, we used a combination of Wilcoxon signed-ranks tests and independent sample Mann–Whitney *U*-tests. As non-parametric tests are less

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powerful than parametric ones, when the significance level was between 0.05 and 0.1, we double-checked results by applying parametric methods to transformed data. In all such cases, the significance of the tests was unaltered.

When individual data were used, we employed generalised linear mixed models (GLMMs) to account for the effect of colony and worker ID. All GLMMs included, at most, two fixed predictor variables. Model selection was based on AIC and always began with the full model, involving interaction. The fit of all GLMMs was validated via analyses of Pearson residuals. All statistical analyses were performed in SPSS (release versions 21.0.0.0, 23.0.0.0, IBM Corporation and others 1989, 2012, 2016).

Tandem running at the colony level

We used a combination of paired-sample *t*-tests for measures with normally distributed data, and Wilcoxon signed-ranks tests for measures where the data were not normally distributed.

Individual tandem running distribution

GLMMs assessing the effect of the number of leading and following attempts on the success of leading and following used leading or following success/failure as the binomial response variables with a logit link, distance (100 or 300 mm) as a fixed factor predictor, number of attempted leads or follows as a covariate, and colony ID as a random factor. Worker ID was redundant, as no repeated measures were taken for any of the individuals. The GLMM assessing the number of attempted tandem runs by workers across emigration involvement groups used the total number of attempted tandem runs as a normal response variable with a log link, distance (100 or 300 mm) and involvement in either or both emigrations as fixed factor predictors, the interaction between the two, and colony ID and worker ID nested within colony ID as random factors. The GLMM assessing per capita attempted tandem running workload used per capita attempted workload as a normal response variable with a log link, distance (100 or 300 mm) and involvement in either or both emigrations as fixed factor predictors, the interaction between the two and colony ID as a random factor. The GLMM assessing per capita successful tandem running workload used successful workload per capita as the normal response variable with a log link, distance (100 or 300 mm) and involvement in either or both emigrations as fixed factor predictors, the interaction between the two, and colony ID and worker ID nested within colony ID as random factors.

We used paired *t*-tests to compare the percentage of individuals involved at both emigration distances with the percentage involved at only one distance for each colony.

Average worker return speeds

A Wilcoxon signed-ranks test was employed to determine differences in the average return speed of workers between the two distances.

Scouting propensity and emigration engagement

The difference in the number of active scouts between distances was tested using a Wilcoxon signed-ranks test. To calculate the tandem running propensity of workers based on previous scouting activity, we measured the number of ants engaging in tandem runs as a proportion of the total population in each scouting category (the two scouting categories were individuals previously involved in scouting, and individuals not previously involved in scouting), within colonies. This was assessed using a combination of Mann–Whitney *U*-tests (leading) and independent sample *t*-tests (following). Differences between the two distances were quantified with a Mann–Whitney *U*-test.

Discovery times and quorum attainment

Distance-based differences in the time to quorum attainment were tested with a paired-sample *t*-test, while differences in new nest discovery time were assessed with a Wilcoxon signed-ranks test.

RESULTS

Tandem running at the colony level

Under the longer distance emigration treatment, colonies on average employed a higher number of tandem runs (Wilcoxon signed-ranks tests, U=2.194, N=10, median_{100}=8.5, median_{300}=14, P=0.028; Fig. 2A). By contrast, the percentage of successful tandem runs was reduced, on average, at the longer emigration distance, although this was not statistically significant (paired-sample *t*-test, t=1.032, d.f.=9, P=0.329; Fig. 2B). Additionally, at the longer emigration distance, colonies utilised a greater percentage of their potential workforce in both tandem running (paired-sample *t*-test, t=48.00, d.f.=9, P=0.037) and the emigration process *in toto* (scouting and tandem running; paired-sample *t*-test, t=−3.214, d.f.=9, P<0.001; Fig. 2C,D).

Individual tandem running distribution

Across both emigration distances, an individual's probability of leading a tandem run successfully significantly increased with the number of leading attempts made (GLMM, odds ratio=1.422, d.f.=140, P=0.017), independent of colony ID (colony random effect: Z=0.918, P=0.359). Furthermore, in agreement with the colony-level data, tandem leaders had a higher probability of success when leading at the shorter distance (GLMM, odds ratio=2.100, P=0.030). However, the number of following attempts had no significant impact on the probability of following success (GLMM, odds ratio=0.216, d.f.=189, P=0.735), independent of the random factor (colony random effect: Z=0.775, P=0.439). The probability of following success was higher, but not statistically significantly so, at the shorter distance (GLMM, odds ratio=1.284, P=0.427).

Across colonies, the percentage of individuals involved (scouting or tandem running) in emigrations at both distances was smaller than the percentage involved at just one distance (paired-sample *t*-test, t=−4.039, d.f.=9, P=0.001; Fig. 3). The interaction between distance and involvement group was significant in its effect on the total number of tandem runs attempted per individual (GLMM, effect of interaction: $F_{1,262}$=4.455, P=0.036; Fig. 4), indicating that worker group was important within distances. Specifically, the 'both' engagement group attempted more tandem runs per individual than the 'either' group at 300 mm (GLMM, Bonferroni *post hoc* test: t=5.098, d.f.=262, P<0.001, $\text{mean}_{\text{either}}$=1.281, $\text{mean}_{\text{both}}$=2.000), but not at 100 mm (GLMM, Bonferroni *post hoc* test: t=1.143, d.f.=262, P=0.254, $\text{mean}_{\text{either}}$=1.145, $\text{mean}_{\text{both}}$=1.316), suggesting a greater role for this group at the longer distance.

Following on from this, the per capita attempted tandem running workload of ants in the 'both' group was significantly higher than that in the 'either' group across both emigration distances (GLMM, effect of group: $F_{1,292}$=18.327, P<0.001, $\text{mean}_{\text{either}}$=0.579, $\text{mean}_{\text{both}}$=0.750). The attempted per capita tandem running workload of the ants was lower at 300 mm than at 100 mm, regardless of their involvement in either or both emigrations (GLMM, effect of distance: $F_{1,292}$=15.149, P<0.001, mean_{100}=0.741, mean_{300}=0.586; Fig. 5A). However, the interaction between distance and involvement group was very

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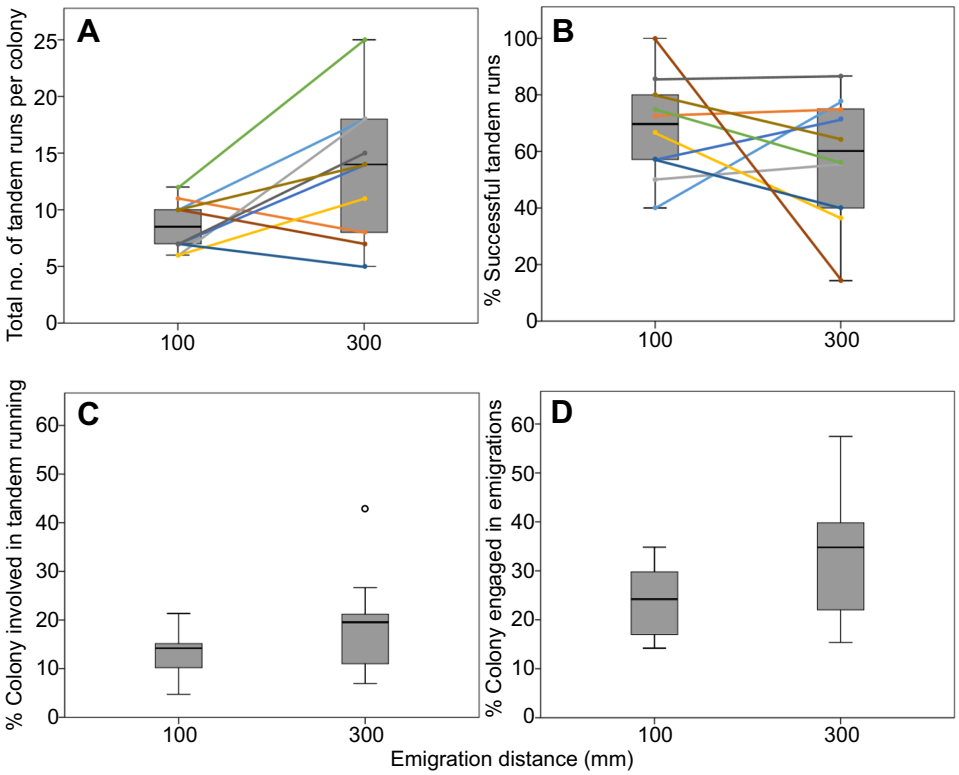

Fig. 2. Tandem run analysis. (A) Total number of tandem runs at the colony level (N_{100}=10, N_{300}=10, P=0.028). (B) Percentage of successful tandem runs of those attempted (N_{100}=10, N_{300}=10, P=0.329). (C) Percentage of the colony engaged in tandem running (N_{100}=10, N_{300}=10, P=0.037). (D) Percentage of the colony engaged in the emigration process as a whole (scouting, tandem leading or following; N_{100}=10, N_{300}=10, P<0.001). Data are for the two emigration distances: 100 and 300 m. Coloured lines indicate individual colony changes in tandem running over the two distances. Outliers (greater than 1.5 times the interquartile range from the median) are indicated with circles.

close to the threshold of significance (GLMM, effect of interaction: $F_{1,292}$=3.817, P=0.052). This may be explained by the per capita workload performed by the 'both' group being significantly higher than that for the 'either' group at 300 mm (GLMM, Bonferroni *post hoc* test: t=4.026, d.f.=292, P<0.001, $\text{mean}_{\text{either}}$=0.486, $\text{mean}_{\text{both}}$=0.708) but not at 100 mm (GLMM, Bonferroni *post hoc* test: t=1.762, d.f.=292, P=0.079, $\text{mean}_{\text{either}}$=0.691, $\text{mean}_{\text{both}}$=0.795).

Interestingly, when only successful tandem running workload was examined, these differences were somewhat diminished; per capita tandem running workload was still lower at 300 mm than at 100 mm across both involvement groups (GLMM, effect of distance: $F_{1,292}$=4.831, P=0.029, mean_{100}=0.737, mean_{300}=0.591; Fig. 5B). Ants in the 'both' group also still had a significantly higher successful per capita tandem running workload than those in the 'either' group across both distances (GLMM, effect of group: $F_{1,292}$=6.037, P=0.015, $\text{mean}_{\text{either}}$=0.582, $\text{mean}_{\text{both}}$=0.748; Fig. 5B); however, the interaction between distance and whether ants were involved in either or both emigrations was not significant (GLMM, effect of interaction: $F_{1,292}$=0.012, P=0.915). This was due to a lack of difference within distances at both 100 mm (GLMM, Bonferroni *post hoc* test: t=1.774, d.f.=292, P=0.077, $\text{mean}_{\text{either}}$=0.654, $\text{mean}_{\text{both}}$=0.831) and 300 mm (GLMM, Bonferroni *post hoc* test: t=1.677, d.f.=292, P=0.097, $\text{mean}_{\text{either}}$=0.519, $\text{mean}_{\text{both}}$=0.673).

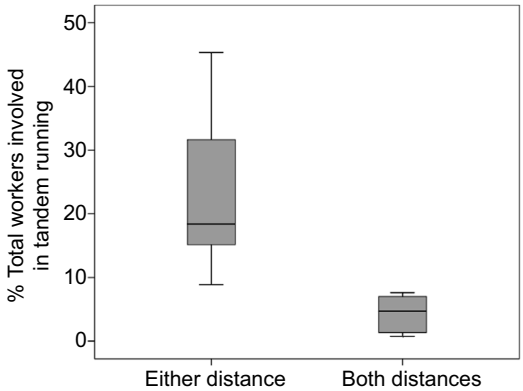

Fig. 3. Number of workers involved in tandem running at one or both emigration distances. Data are given as a percentage of the total number of workers actively engaged for both groups. Actively engaged workers are those involved in scouting, tandem leading or following (N_{100}=10, N_{300}=10).

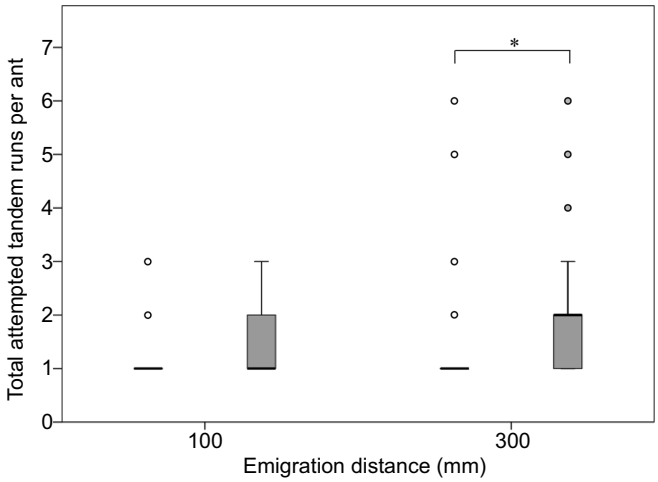

Fig. 4. Total number of attempted tandem runs per individual worker. Boxplots are divided by emigration distance and, within each distance, by individuals actively engaged at only that distance ['either' group, white (flat) boxes] or both distances ('both' group, grey boxes) (N=296: $N_{100,\text{either}}$=76, $N_{100,\text{both}}$=53, $N_{300,\text{either}}$=114, $N_{300,\text{both}}$=53). Asterisks indicate significant differences within distances (Bonferroni *post hoc* test, P<0.05). Outliers (greater than 1.5 times the interquartile range from the median) are indicated with circles.

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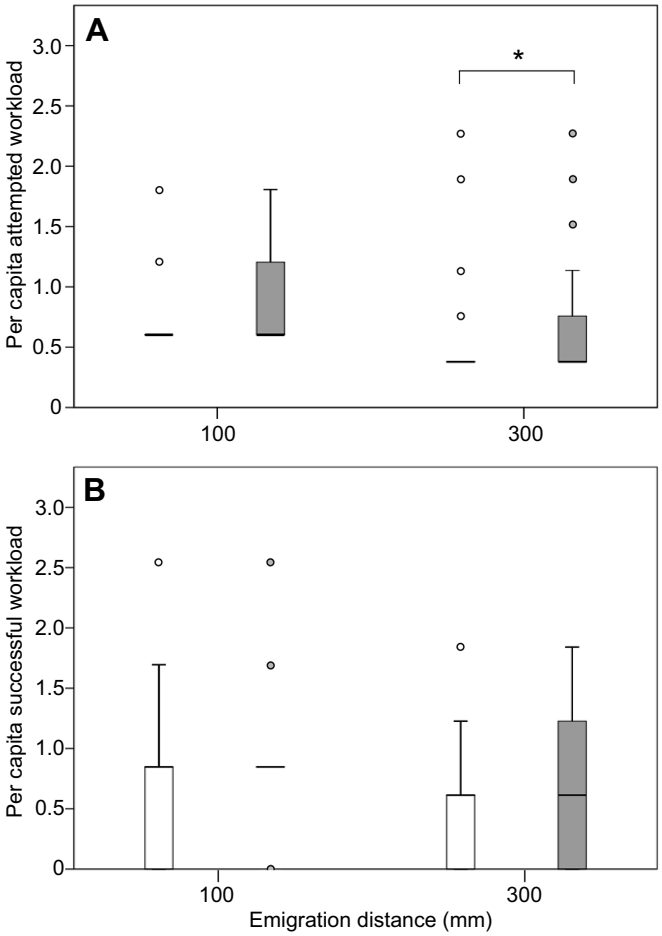

Fig. 5. Workload per ant. (A) Per capita attempted workload. (B) Per capita successful workload. Boxplots are divided by emigration distance and, within each distance, by individuals actively engaged at only that distance ('either' group, white boxes) or both distances ('both' group, grey boxes) (N=296: $N_{100,either}$=76, $N_{100,both}$=53, $N_{300,either}$=114, $N_{300,both}$=53). The asterisk indicates a significant difference within distance (Bonferroni *post hoc* test, P<0.05). Outliers (greater than 1.5 times the interquartile range from the median) are indicated with circles.

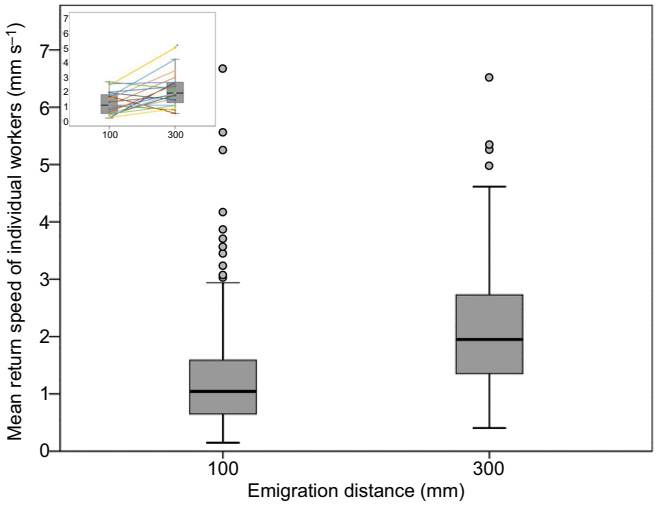

Fig. 6. Mean return speed of workers within colonies for the two distances. Boxplots are divided by emigration distance (N_{100}=101, N_{300}=114, P<0.001). Outliers (greater than 1.5 times the interquartile range from the median) are indicated with circles. The inset displays changes in mean return speed of individuals tracked across both emigration distances; coloured lines indicate each individual's change in mean return speed (N_{100}=20, N_{300}=20).

Average worker return speeds

The average return speed of workers across colonies was significantly higher for longer emigration distances (Wilcoxon signed-ranks test, U=−3.92, N=10, P<0.001; Fig. 6).

Scouting propensity and emigration engagement

Before emigrating over the longer distance, on average, colonies employed a significantly greater number of scouts (Wilcoxon signed-ranks test, U=2.253, N=10, P=0.024, mean_{100}=16, mean_{300}=25). In any given emigration, previous scouting significantly increased a worker's propensity both to lead (Mann–Whitney U-test, U=3.250, N_{scouted}=10, $N_{\text{not-scouted}}$=10, P<0.001, $\text{median}_{\text{scouted}}$=0.176, $\text{median}_{\text{not-scouted}}$=0.040) and to follow (independent-sample t-test, t=−3.680, d.f.=9, P=0.002, $\text{mean}_{\text{scouted}}$=0.172, $\text{mean}_{\text{not-scouted}}$=0.084) tandem runs, and this trend was not significantly different between emigration distances (Mann–Whitney U-test, leading: U=0.338, N_{100}=10, N_{300}=10, P=0.738, median_{100}=0.071, median_{300}=0.084; following: U=1.826, N_{100}=10, N_{300}=10, P=0.068, median_{100}=0.073, median_{300}=0.137); however, it should still be noted that the median for following was much higher at 300 mm.

Discovery times and quorum attainment

The time to quorum attainment was significantly later in emigrations over longer distances (paired-sample t-test, t=−3.565, d.f.=9, P=0.006, mean_{100}=39.41 min, mean_{300}=94.22 min). However, though later in the distant treatment, nest discovery time was not significantly affected (Wilcoxon signed-ranks test, U=9.811, N=10, P=0.114, median_{100}=13.37 min, median_{300}=31.54 min, checked with a paired t-test after $\log_{10}$ transformation, P=0.087), probably in part due to the increased rate of scouting.

DISCUSSION

Our results show that in *T. albipennis* colonies, tandem running activity is redistributed across individuals in response to differing emigration distances. In agreement with previous work (Pratt et al., 2002; Pratt, 2004; O'Shea-Wheller et al., 2016), we found that the incidence of tandem running rose significantly with longer emigration distances (Figs 2A,C and 4). Tandem success tended to decrease with distance, although this result was statistically significant only for leaders; it was not significant either for followers or for colonies as a whole (Fig. 2B). Furthermore, a significantly larger proportion of each colony was engaged in emigrations and tandem running at 300 mm than at 100 m, and average worker return speeds were higher at 300 m (Figs 2C,D and 6). Crucially, we observed that a small minority of individuals attempted a greater workload (leading or following tandem runs) at the longer emigration distance in comparison to their nest mates (Fig. 5A). However, the relative importance of these ants dwindled when only successful workload was considered (Fig. 5B). In concert, our data show that while colonies use multiple processes to adjust emigration dynamics over longer distances, an increase in the number of active individuals is likely to be the key driver behind increased tandem running (Fig. 2C,D).

The upregulated investment in tandem running over longer emigration distances may be explained by the lower independent discovery rate of more distant nests (O'Shea-Wheller et al., 2016; Pratt, 2004). This is because to commit to a new nest, colonies must achieve a quorum threshold, which may be attained by ants

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individually discovering a new nest or being recruited to it via tandem running (Pratt, 2004). Consequently, a decrease in individual discovery rate seems to require an increase in tandem running to reach such a quorum (Fig. 2A). Interestingly, average worker return speed also increased, and the explanation for this probably relates to the properties of ant locomotion; it has been shown that for any given movement, the longer the duration, the higher the average speed (Fig. 6) (Christensen et al., 2015). However, while every movement is bracketed by an initiation and termination phase, these phases comprise a constant percentage of the overall movement, suggesting that ants determine movement duration before initiating a journey (Christensen et al., 2015). Consequently, this indicates that ants up-regulate their speed when planning to move over longer distances (Hunt et al., 2016). Previous studies have found that this speed–distance rule applies to short discrete movements, yet the majority of journeys are made up of many such movements. Here, to our knowledge for the first time, we show that it is also applicable to longer, compound movements, indicative of a consistent overarching mechanism.

Differences at the colony level were underpinned by variation in individual behaviour between emigration distances. The finding that individual tandem running workload (leading and following tandem runs) decreased with the number of ants actively engaged (Figs 5 and 2D) is consistent with observations in analogous systems, and constitutes a commonly observed phenomenon in insect societies (Karsai and Wenzel, 1998; Dornhaus et al., 2008). Principally, the decrease in individual contributions when more ants are engaged may be explained by the reduced need for workers to be involved in a task, and the concomitant reduction in task stimuli (Pinter-Wollman et al., 2012). Furthermore, for longer emigrations, although more tandem runs may be required because of a reduced encounter rate (O'Shea-Wheller et al., 2016; Pratt, 2004), colonies of *T. albipennis* use quorum thresholds relative to their total population (Dornhaus and Franks, 2006). As such, the quorum threshold required by a colony of any given size should remain constant, and thus the task of attaining it would potentially be distributed over more workers at longer emigration distances, creating a dilution of individual effort (Dornhaus and Franks, 2006).

The change in the number of tandem runs between distance treatments might largely be attributed to the greater number of workers engaging in more distant emigrations. However, in concert with this, some ants that were involved in multiple emigrations conducted many more tandem runs at 300 mm than the rest of the actively engaged worker population (Fig. 4). This suggested that there were certain individuals specialising in the task, as is the case for other task groups in this species (Robinson et al., 2009; Pinter-Wollman et al., 2012). As such, there was the potential for these individuals to contribute significantly to the tandem running process, via task threshold differences and reinforcement processes (Sendova-Franks et al., 2002; Sendova-Franks and Franks, 1995). The idea of task reinforcement was supported further by the finding that more leading attempts did correlate with a higher success rate, and so we investigated the relative contributions of worker groups actively engaged in emigrations, in an effort to isolate a specialist faction.

We defined actively engaged workers as those conducting scouting, leading or following of tandem runs, or both. This definition was adopted as previous scouting activity significantly increased an individual's propensity to either lead or follow tandem runs, a trend that remained constant across both distances, although was more probable at 300 mm. We separated actively engaged workers into two groups: workers actively engaged across both distances and workers actively engaged at only one distance. This division method allowed us to determine how individuals recurrently involved in emigrations contributed to the process. This group formed a minority of the total population of actively engaged workers (Fig. 3) but, interestingly, attempted a significantly greater number of tandem runs per individual (Fig. 4). Furthermore, ants in this group attempted a significantly greater workload per individual than those in the 'either' group, when migrating over the longer distance (Fig. 5A). However, the data for successful workload per individual did not differ significantly between the two groups, at any distance (Fig. 5B).

Our data suggest that some individuals are indeed disproportionately active in the tandem running process, specifically attempting more tandem runs per ant overall (Fig. 4), and a greater per capita workload when the new nest is further away (Fig. 5A). However, they do not perform a greater successful workload per capita within distances (Fig. 5B), and as such, the relative importance of these 'elite' workers (Hölldobler and Wilson, 1990) in shaping emigration dynamics is debatable. Instead, it appears that the majority of changes in tandem running at the colony level are achieved via increased recruitment of workers into the process, rather than by reliance on key individuals (Figs 2C,D and 5B). Such findings are also supported by previous work, showing that the ability to utilise a larger workforce negates the need for specialists (Dornhaus et al., 2009). This highlights an interesting contradiction; it suggests that although some workers are highly active and conform to the definition of 'elites', they may not actually be that effective at their task, despite investing more effort than their nest mates. Indeed, a recent study, also in the *Temnothorax* genus, found that reliance on specialists in the face of dynamic environments may be disadvantageous (Jongepier and Foitzik, 2016), highlighting another case in which the contribution of 'elites' is far from decisive.

The presence of inactive or 'lazy' workers has received some attention in social insects (Dornhaus et al., 2008; Beshers and Fewell, 2001) and may be accounted for proximately by task thresholds, as inactive individuals are likely to be those that require a higher level of stimulus before they engage in a given task (Robinson et al., 2009). However, here we see a case of active but ineffective workers in a task that is moderately difficult to complete (only 65% of all tandem runs were successful). While the exact mechanisms underlying this are as yet unknown, there are several potential causes. One possibility is that workers attempting a greater number of tandem runs were doing so as a compensatory reaction to failing more often. This is plausible, as interruptions to tandem runs were common in our experiment, as in others (Franks et al., 2009). It is also likely that highly active individuals made a significant contribution by leading only partially successful tandem runs. This is because, as demonstrated in previous experiments (Franks et al., 2010), even when tandem runs end prematurely, they may still be effective in directing naive workers to a new nest (Franks et al., 2010; Pratt, 2008). However, while both of these factors provide viable explanations, their relative importance will probably require further investigation.

In conclusion, we found that several factors contribute to the acceleration of emigrations over longer distances, and that both highly active individuals and the regulation of total worker involvement play a role. Crucially, we show that the greater number of active workers employed over longer emigrations is the strongest factor linked to increased tandem running, having a greater influence than the utilisation of 'elite' workers. Overall, our results indicate that although key individuals have their place

in the tandem running process, it is the mobilisation of the masses that is likely to make the real difference when emigrating over greater distances.

Competing interests
The authors declare no competing or financial interests.

Author contributions
T.A.O.-W. and N.R.F. conceived the study and wrote the manuscript; T.A.O.-W., D.K.W.-A. and D.E.E. conducted all experimental work; T.A.O.-W. and A.B.S.-F. carried out the statistical analysis. All authors gave final approval for publication.

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